

A review of the classification of *Acacia* (Leguminosae, Mimosoideae)

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Abstract

This paper reviews the history of the systematics of *Acacia s.l.*, providing a comparison of recent phylogenies to previous classifications, with a focus on *Acacia s.s.* Herein, *Acacia s.s.* is used in the sense of the segregated genus based on *A. penninervis*, and excluding *Senegalia*, *Vachellia*, *Acaciella*, and *Mariosousa*. Problems have been apparent with the classification of *Acacia s.l.* for many years and there is now general recognition that *Acacia s.l.* is polyphyletic. *Acacia s.s.*, a largely Australian group with close to 1000 species, has been shown to be monophyletic. Although molecular phylogenetic studies in recent years have clarified the relationships of some groups within *Acacia s.s.*, this diverse clade lacks a phylogenetic classification. Recent evidence has provided renewed support for the recognition of a redefined section *Pulchelloidea sensu* Vassal, and although formal taxonomic changes at this time are regarded as premature, it has been demonstrated that taxonomic groups in *Acacia s.s.* based upon one or two "key" characters are not monophyletic.

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Introduction

The genus *Acacia* Miller, if treated in the broad sense, includes c.1450 species (Lewis *et al.* 2005, p. 3) with species in Africa, the Americas, Asia and Australia, and forms the second most speciose genus in the family Leguminosae after *Astragalus* (Maslin 1988; Mabberley 1997). If treated in the strict sense following the re-typification of *Acacia* with an Australian type (Orchard & Maslin 2003; Maslin 2008), *Acacia s.s.* (formerly *Acacia* subgenus *Phyllodineae*, synonym *Racosperma*), includes 987 species (see Fig. 1 for distribution) with 975 species in Australia (Maslin 2004), and is still the second largest legume genus by a considerable margin (Lewis *et al.* 2005). *Acacia s.s.* comprises the largest genus of plants in Australia (Maslin 1995). No species currently occur in New Zealand, although fossil evidence suggests that the genus was once present there (Guinet 1981; Martin 1994). Several species of *Acacia s.l.* are common in the Middle East, and references to members of the genus date from early in recorded history. For example, the ancient Egyptians had a hieroglyphic symbol for *Acacia*, and the Bible describes the Ark of the Tabernacle as being made of *Acacia* wood (Moldenke & Moldenke 1952). It is not surprising that a group of plants known from such early times has such a long and complex systematic history.

Herein the segregated generic names for *Acacia s.l.* will be used following the re-typification of *Acacia* with an Australian type, namely: *Acacia s.s.* (formerly *Acacia* subgenus *Phyllodineae*, synonym *Racosperma*), *Vachellia* (formerly *Acacia* subgenus *Acacia*), *Senegalia* (formerly *Acacia* subgenus *Aculeiferum s.s.*), *Acaciella* (formerly *Acacia* subgenus *Aculeiferum* section *Filicinae*), and *Mariosousa* (formerly *Acacia* subgenus *Aculeiferum* "Acacia coulteri group"). Further explanation of these names and their application can be found in Maslin (2008). However, when comparing alternative classifications and results, the original names used by each author are retained (where possible), to simplify the summary of the original literature.

In recent times the need for a phylogenetically based classification of *Acacia s.l.*, to guide workers in a variety of fields, has become increasingly apparent. Examples include studies of host-parasite co-evolution (Crespi *et al.* 2004); plant physiology (Pohlman 2005; Warwick & Thukten 2006);



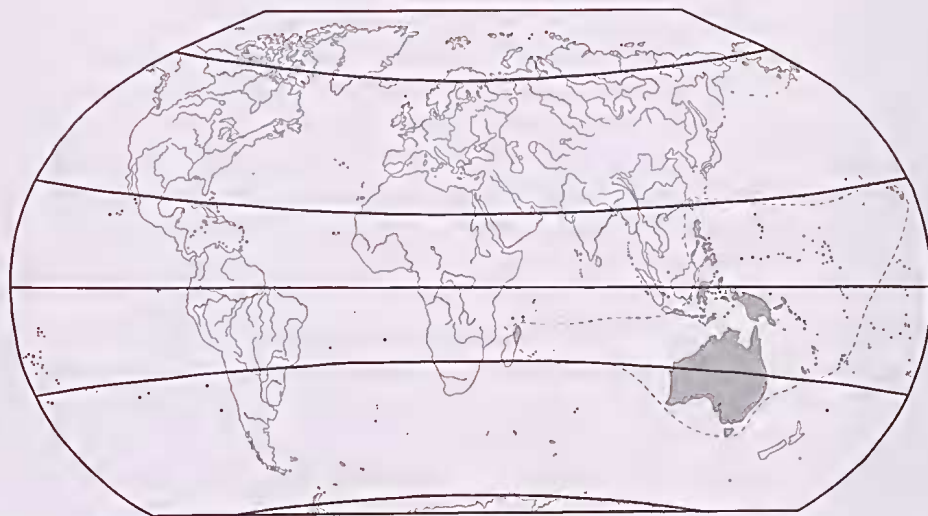


Figure 1. Distribution map of *Acacia s.s.*, also described as the “Australian group” (formerly *Acacia* subgenus *Phyllodineae*, synonym *Racosperma*).

and rhizobial interactions and atmospheric nitrogen fixation (Brockwell *et al.* 2005). Because it is such a large and heterogeneous group, *Acacia s.s.* has a particular need for an infrageneric classification based on phylogenetic principles. Currently the most frequently used classification, of Pedley (1978), combines earlier schemes, such as those of Bentham (1875) and Vassal (1972), in an attempt to create a pragmatic system (Maslin 2001). This classification was adopted (albeit slightly altered, with section *Alatae* not recognised) by Maslin (2001), in the comprehensive *Flora of Australia* treatment of *Acacia s.s.* Maslin (2001) acknowledged that this was not a phylogenetically based classification, but it provided a pragmatic subdivision of the genus. In this paper an overview of previous classifications of *Acacia s.l.* is provided. There have been several recent reviews (e.g. Chappill & Maslin 1995, Maslin & Stirton 1997, Maslin 2001, Maslin *et al.* 2003a, 2003b) and this paper aims to extend these reviews to take into account the results of recent molecular systematic studies. New molecular analyses have increased our knowledge of the phylogeny of *Acacia s.l.* dramatically (notably Luckow *et al.* 2003; Murphy *et al.* 2000, 2003, 2005; Miller *et al.* 2003a, 2003b; Brown *et al.* 2006; Ariati *et al.* 2006). The aim of this paper is to provide a review of the systematics of *Acacia s.l.*, with a particular focus on *Acacia s.s.*, with a guide to pertinent literature on

systematics, classification and recent phylogenetic analyses. In order to follow the complex nomenclature, a table comparing the main classification schemes and a broad comparison of ranks and names is provided for *Acacia s.s.* (Table 1).

Mimosoideae: some background

Acacia s.l. is placed in the legume subfamily Mimosoideae, in tribe Acacieae (Lewis 2005). In the latest comprehensive classification of Leguminosae, the Mimosoideae comprise c. 3270 species in four tribes (Lewis *et al.* 2005), rather than the five tribes recognised in Mimosoideae (Bentham 1875; Elias 1981) until recently. Some recent morphological and molecular datasets have supported the monophyly of the Mimosoideae (Chappill 1995; Käss & Wink 1996; Dayanandan *et al.* 1997; Lavin *et al.* 2005), characterised by regular (actinomorphic) flowers with valvate petals often fused at the base and compound pollen with porate apertures (Polhill *et al.* 1981; Guinet 1981). Chappill (1995) listed a number of morphological synapomorphies found in most (but not all) taxa in the Mimosoideae clade, including bipinnate leaves, abaxial position of the median petal, valvate petal aestivation, prominently exerted stamens, four celled polyads and absence of a styler groove. However, Elias (1981), and

Table 1. A comparison of the classification schemes of *Acacia s.s.* (formerly *Acacia* subgenus *Phyllodineae*, synonym *Racosperma*) by Bentham (1875), Vassal (1972), Pedley (1978), Pedley (1986), Maslin and Stirton (1997) and Maslin (2001), modified from Chappill and Maslin (1995) and Murphy *et al.* (2003). Where possible equivalent groups (at different ranks) are aligned from left to right across table. This comparison has not been possible to maintain between all classifications, and some incongruities are noted in square brackets. Abbreviations: gen. = genus; ser. = series; subser. = subseries; subg. = subgenus; sect. = section; subsect. = subsection.

Bentham (1875)	Vassal (1972)	Pedley (1978)	Pedley (1986)	Maslin and Stirton (1997)	Maslin (2001)
	subg. <i>Heteraphyllum</i>	subg. <i>Phylladineae</i>	gen. <i>Racosperma</i>	subg. <i>Phylladineae</i>	subg. <i>Phylladineae</i>
	(Syn subg. <i>Phylladineae</i>)				
ser. <i>Batrycephalae</i>		sect. <i>Batrycephalae</i>	sect. <i>Racosperma</i> [synonymy includes sections <i>Phylladineae</i> , <i>Alatae</i> and <i>Batrycephalae</i> of Pedley (1978)]	sect. <i>Batrycephalae</i>	sect. <i>Batrycephalae</i>
ser. <i>Pulchellae</i>	sect. <i>Pulchellaidea</i>	sect. <i>Pulchellae</i>	sect. <i>Pulchellae</i>	sect. <i>Pulchellae</i>	sect. <i>Pulchellae</i>
ser. <i>Phylladineae</i>					sect. <i>Phylladineae</i>
subser. <i>Alatae</i>	subsect. <i>Parviscutellae</i>	sect. <i>Alatae</i>		sect. <i>Alatae</i>	
subser. <i>Cantinuae</i>	subsect. <i>Magniscutellae</i>				
subser. <i>Uninerves</i>	sect. <i>Uninervea</i>	sect. <i>Phylladineae</i>		sect. <i>Phylladineae</i>	
				a. "Racemase species" b. "Nan-racemase species"	
subser. <i>Plurinerves</i>	sect. <i>Heteraphyllum</i>	sect. <i>Plurinerves</i>	sect. <i>Plurinervia</i>	sect. <i>Plurinerves</i>	sect. <i>Plurinerves</i>
subser. <i>Pungentes</i>	subsect. <i>Glabuliferae</i>			a. "Microneurus species" b. "Oligoneurus species"	
subser. <i>Calamiferae</i>					
subser. <i>Juliflariae</i>	subsect. <i>Spiciferae</i>	sect. <i>Juliflariae</i>		sect. <i>Juliflariae</i>	sect. <i>Juliflariae</i>
				a. "Microneurus species" b. "Oligoneurus species"	
subser. <i>Bruniidae</i>	[rank not used]	sect. <i>Lycopadiifaliae</i>	sect. <i>Lycopadiifalia</i>	sect. <i>Lycopadiifalia</i>	sect. <i>Lycopadiifalia</i>

Luckow *et al.* (2000) found that the Mimosoideae are not monophyletic due to uncertainty surrounding the relationships of some taxa of the *Dimorphandra* group of Caesalpinioideae, and a number of other studies have found Caesalpinioideae to be paraphyletic (Chappill 1995; Käss & Wink 1996; Doyle *et al.* 1997). The distinction between taxa in the Caesalpinioideae and Mimosoideae is not well defined and further phylogenetic analysis is required to clarify this boundary (Luckow *et al.* 2005a).

Mimosoideae were traditionally composed of five tribes: Parkieae, Mimosygantheae, Mimoseae, Ingeae and Acacieae (Bentham 1875; Elias 1981). *Acacia s.l.* species make up over one third of the members of the Mimosoideae (Cowan 1998). All five tribes were characterised by floral features, although the genera included in each tribe have often changed according to the interpretations of different authors. It is notable that the "defining characters" may not be present in all genera assigned to a particular tribe. Elias (1981) defined the Parkieae as having an imbricate calyx in the bud (although in that volume *Parkia* and *Pentaclethra*, were mistakenly noted as having valvate aestivation of the calyx lobes). Parkieae were further characterised by sepals united into a tube, five or ten stamens with staminodia, and anthers with or without an apical gland. DNA sequence data from the *rbcl* gene have been insufficient to resolve the relationship of Parkieae to the other tribes in the Mimosoideae (Käss & Wink 1996; Dayanandan *et al.* 1997). Luckow *et al.* (2000) found that Parkieae was polyphyletic, with *Pentaclethra* removed from *Parkia* at a basal node in the Mimosoideae, and both genera are now known to be related to different genera in the Mimoseae (Luckow *et al.* 2005a). In the classification of Luckow (2005) this has resulted in the inclusion of both *Pentaclethra* and *Parkia* in the Mimoseae and the abandonment of Parkieae as a tribe. The tribe Mimosygantheae was characterised by imbricate free sepals, ten functional stamens and no anther gland; it is monotypic, containing only *Mimosyganthus carinthus*. Unlike Parkieae, Mimosygantheae was retained in Lewis *et al.* (2005) despite recent molecular phylogenetic results showing this genus to be nested in Mimoseae, sister to *Prosopidastrum*.

The remaining three large tribes of Mimosoideae traditionally recognised comprise: the Mimoseae, which were characterised by valvate calyx aestivation

and twice as many stamens as petals (Lewis & Elias 1981); the Ingeae, which had valvate calyx lobes and numerous stamens fused into a tube (Nielsen 1981; for a full overview see Brown 2008); and the Acacieae, which were characterised by an indefinite number of stamens (more than 10) that are free or united only at the base and a calyx that is valvate in the bud (Elias 1981; Vassal 1981). These features, however, are not unique to the tribe. In fact, no single morphological character distinguishes Acacieae from other tribes in subfamily Mimosoideae, and this has called into question the monophyly of Acacieae and the other tribes in the Mimosoideae (Chappill & Maslin 1995). Chappill and Maslin (1995) found members of the Mimoseae to be sister to a clade containing Parkieae, Ingeae and Acacieae, although they acknowledged that many characters were missing in their analysis. Acacieae includes *Acacia s.l.*, and the monotypic genus *Faidherbia* A. Chev., although there is some ongoing debate as to whether *Faidherbia* is better placed in the tribe Ingeae (Elias 1981; Guinet 1990; Lewis & Rico-Arce 2005).

Species of *Acacia s.l.* are generally trees or shrubs; some African and American species, however, have a scandent habit (Ross 1981). Most have free staminal filaments, although some African and American species have filaments that are shortly united at the base. Much debate has centred around whether *Acacia s.l.* is monophyletic or if it contains multiple lineages and should be split into more than one genus (e.g. Pedley 1986; Maslin *et al.* 2003b). Chappill and Maslin (1995) found *Acacia s.l.* to be paraphyletic based on morphological and chemotaxonomic characters, but they did not recommend taxonomic revision until further research had been completed because such a split would require far-reaching nomenclatural changes (Maslin 1987, 1988; Chappill & Maslin 1995). In the past decade it became clear that any attempt to resolve the relationships of *Acacia s.l.* needed to include members of other Mimosoideae tribes, in particular the Ingeae (Chappill & Maslin 1995; Grimes 1995; Robinson & Harris 2000). It was not until more comprehensive sampling of the other tribes in Mimosoideae was done, that Ingeae and Mimoseae were also recognised as non-monophyletic (Luckow *et al.* 2003; Miller *et al.* 2003b). It has recently been found, on the basis of molecular phylogenetic analyses, that the tribal system of

Mimosoideae is in need of complete revision, with the current tribes polyphyletic or paraphyletic (Luckow *et al.* 2003). The non-monophyly of Acacieae and Ingeae are particularly problematic, with the recognition of monophyletic taxa requiring the generic revision of *Acacia s.l.* (Miller *et al.* 2003b). This has contributed to a highly controversial debate about the application of the name *Acacia* (Pedley 1986; Maslin *et al.* 2003a; 2003b, Luckow *et al.* 2005b). The recent classification of Mimosoideae presented in Lewis *et al.* (2005) was a stop-gap measure and recognised four rather than five tribes in Mimosoideae, mainly based on the results of Luckow *et al.* (2000 and 2003). In other respects the Lewis *et al.* (2005) classification largely retains the scheme of Elias (1981) in recognising the four tribes, Mimoseae, Mimosygantheae, Ingeae and Acacieae, but not Parkieae, despite acknowledgment that these tribes (apart from the monotypic Mimosygantheae) are not monophyletic. It is evident that the higher level classification of the Mimosoideae is still fluid pending further comprehensive phylogenetic analysis, but in the meantime the tribal system of Elias (1981) remains a helpful communication device.

A review of the systematic history of *Acacia s.l.*

Early systematic history

The name *Acacia* has been utilised in herbals since the 14th century and was used by Linnaeus as a genus in 1747. These references, however, predate 1753, the starting point of modern botanical nomenclature, and therefore have no formal taxonomic standing today (Ross 1980). Philip Miller (1754) is the author of the name *Acacia*. The original diagnosis included 24 species in the genus and described *Acacia* as having:

“...a tubulous flower, consisting of one leaf, with many stamina or threads, which are many of them collected into a kind of sphere or globe: the point of the flower afterward becomes a pod, in which are included several seeds, each of which is separated by transverse diaphragms, and are generally surrounded with a sweetish pulp” (Miller 1754).

This description was broad, and many species described under *Acacia* in Miller's time are no longer recognised as belonging to *Acacia s.l.* today (Ross 1973). A survey of the pre-Linnean history of *Acacia s.l.* was provided by Ross (1980).

Subsequent to Miller, the number of species in *Acacia s.l.* grew rapidly as many taxonomists named and listed new species. For practical reasons it was soon necessary to subdivide the genus into infrageneric groups. Willdenow (1806) listed 102 species of *Acacia s.l.* and recognised seven groups based on the vegetative characters of foliage type and stipule presence. Willdenow's primary groupings were based on whether the foliage was simple (phyllodinous), pinnate, or bipinnate. Sprengel (1826) included 188 species in *Acacia s.l.* These were divided into three unranked groups according to foliage, in a similar manner to Willdenow (1806). In 1825, de Candolle recognised 258 species in *Acacia s.l.* and divided these into four sections. New (1984), reported that de Candolle used only leaf characters in his classification, but de Candolle in fact recognised these sections on the basis of both floral and foliage characters. As already noted by Pedley (1987a), de Candolle's concept of *Acacia s.l.* was somewhat less confused than Willdenow's, due to the former's use of inflorescence type, but a third of the species listed by both authors are no longer recognised in *Acacia s.l.*

Wight and Arnott (1834) segregated *Acacia farnesiana* into a new genus, *Vachellia*. This separation was clearly based on the distinctive pod of this species, although Pedley (1986) suggested that Wight and Arnott gave no reason for the split. Pedley (1987a) observed that this split began a trend to fragment *Acacia s.l.* which would have resulted in taxonomic chaos were it not for Bentham.

Bentham and *Acacia s.l.* taxonomy in the 19th century

In 1841, Bentham began to re-organise Mimosoideae (which he ranked as a suborder of Leguminosae), recognising Acacieae as one of three tribes. In a series of papers published in the period 1842–1846, Bentham initially recognised ten genera in Acacieae (Bentham 1842a, 1842b, 1844a, 1844b, 1845, 1846). Subsequently, he made radical changes to this classification, restricting Acacieae to one genus, *Acacia s.l.*, and creating the new tribe Ingeae to delimit the other nine genera (Bentham 1865).

Bentham (1842a, 1842b) was the first to clearly restrict the boundaries of the genus *Acacia*, advocating floral characters to define a more natural group. Previous authors had used the presence of a dry, two-valved pod to distinguish *Acacia s.l.* Bentham described

this as an inconvenient and uncertain character due to the absence of pods on herbarium material. By excluding from *Acacia s.l.* all species with definite stamens or filaments connected in a cylindrical tube, Bentham created a much more tightly delimited group than his predecessors, and his concept of *Acacia s.l.* was essentially the same as that used today.

Within *Acacia s.l.*, Bentham (1842a) listed 432 species and defined six series: *Phyllodineae*, *Botrycephalae*, *Pulchellae*, *Gummiferae*, *Vulgares* and *Filicinae*. These series were based primarily on "leaf" or foliage characters and the presence of either stipular spines or prickles (prickles have no vascular tissue, unlike stipules). In his final revision of the genus, Bentham (1875) maintained the above classification (see Table 1), although he raised some unranked groupings within the series *Phyllodineae* to subseries level and reduced the five subseries in *Vulgares* to four. Bentham's subseries were based on inflorescence or vegetative characters and although Bentham did refer to the groups within *Acacia s.l.* as "subgenera" (Bentham 1875, p. 354), in effect predicting what future workers would conclude c. 100 years later, he conformed to the rules governing taxonomic ranks at that time and used the rank of series.

Bentham's classification remained almost intact for the next century and grew to accommodate over twice the number of species. It has been the basis for most subsequent re-arrangements of *Acacia s.l.* (e.g. Guinet 1969; Vassal 1972; Pedley 1978, 1986), and these have, in essence, been re-alignments of Bentham's series, based on changing ideas of taxonomic ranks.

The early 20th century

Bentham was the last taxonomist to revise all known species in *Acacia s.l.* (Pedley 1987a). Since then, authors have proposed changes to infra-generic groups by examining either a limited range of species within previously named sections of *Acacia s.l.* or species in a particular geographic region. In the first half of the 20th century this resulted in two notable challenges to Bentham's (1875) classification.

Britton and Rose (1928) divided *Acacia s.l.* into 12 genera using pod characters of American species. This system was abandoned after Rose's death in 1934, and species described transferred back to *Acacia s.l.* Pedley (1986) wrote that Britton and Rose's classification was

most likely rejected due to problems with recognising genera based on pod characters, and Maslin (1988) described their treatment as "excessive". Britton and Rose renamed Bentham's series *Filicinae* as the genus *Acaciella*, and Pedley (1987b) also later accepted this as a probable distinct genus. *Acaciella* has recently been reinstated and new taxa described within it by Rico Arce and Bachman (2006).

Newman (1932) criticised Bentham's (1875) classification as being "too static" (although he did not explain what this meant) and proposed dividing *Acacia s.l.* into three unranked groups on the basis of a hierarchy of three characters: inflorescence type (racemes, clusters or single inflorescences), flower-groups (cylindrical shaped spikes, oblong spikes or globular heads) and foliage type (bipinnate leaves, phyllodes or absence of leaves). Newman's system was rejected by subsequent authors. New (1984) described it as clearly unnatural, and Pedley (1978) considered it hardly worthy of serious consideration. Newman did, however, recognise the need for a natural classification of *Acacia s.l.*

The second half of the 20th century

Since the 1960s a number of authors have proposed changes to Bentham's (1875) classification, most notably Vassal (1972) and Pedley (1978, 1986) (Table 1). These changes have broadly corresponded to the series and subseries of Bentham, although putatively based more on relationships (although non-cladistic) than those of previous authors.

The classifications undertaken in the past c.40 years were triggered by Guinet's (1969) monumental pollen studies of the polyads of 250 species across all *Acacia s.l.* From this study, Guinet concluded that Bentham's series could be placed into groups based on pollen types. All *Acacia s.l.* are characterised by compound pollen, with a varying number of individual pollen grains. Three pollen types were distinguished by Guinet (1969, 1990):

1. Colporate type: an exine with well-developed columellae and complex apertures composed of a furrow in the external exine and a pore in the internal exine below the furrow.
2. Simple porate type: exine sometimes with weakly developed collumellae. The apertures are simple circular pores on the angles of the distal faces of the pollen grains.

3. Extraporate type: as in the simply porate type, the exine sometimes with weakly developed collumellae and simple pores. The extraporate type is distinguished by false furrows (pseudocolpi) present on the distal faces of the pollen grains.

Guinet (1969) found that the colporate type only occurred in (Bentham's) series *Gummiferae*. The simple porate type was in series *Filicinae*, *Vulgares* and some *Phyllodineae*, while the extraporate type was in *Pulchellae*, *Botrycephalae*, most *Phyllodineae* and some *Vulgares*. Guinet (1986, 1990) later extended his work to cover c. 900 taxa in *Acacia s.l.* Pollen data played an important role in subsequent studies of the systematics of *Acacia s.l.* (Vassal 1972, 1981; Ross 1973; Pettigrew & Watson 1975; Guinet & Vassal 1978; Pedley 1978, 1986), but have been relatively neglected in recent years. Molecular systematics results have not yet been well integrated with the pollen data of Guinet (1969, 1986, 1990).

1. Vassal: three subgenera within *Acacia s.l.*

Vassal (1972) used pollen data, in conjunction with his own work on morphology and ontogeny of seeds and seedlings, to formalise Guinet's (1969) groups. Vassal divided *Acacia s.l.* into three subgenera: subg. *Acacia*, subg. *Aculeiferum* and subg. *Heterophyllum* (although Ross (1981) showed that the name *Phyllodineae* has priority over *Heterophyllum*). These subgenera have formed the conceptual backbone of subsequent classifications (e.g. Guinet & Vassal 1978; Pedley 1978, 1986). Vassal's (1972) groupings are comparable to Bentham's (1875) series, which, as already observed by Pedley (1978), was fortunate, since many of the characters Vassal used for his classification – such as seedling and pollen morphology – are not easily observable. Following Guinet (1969), Vassal (1972, 1979) referred the African species *Acacia albida* to the monotypic genus *Faidherbia* on the basis of its distinctive pollen morphology (polyads with 30 grains compared to 16 grains in all but one African species) and its unique seedling ontogeny (it produces bipinnate leaves from the outset – all other species first develop pinnate leaves). Vassal (1972), however, did not remove *Faidherbia* from the Acaciaeae, contrary to Guinet's (1969) assertion that it would be better placed in the Ingeae because it was, in his opinion, not closely

related to the genus *Acacia s.l.* Vassal (1981) maintained *Faidherbia* in the Acaciaeae, although Elias (1981) in the same volume stated that the genus was better placed in the Ingeae. This argument has not been finally resolved, although in the classification of Lewis and Rico-Arce (2005), *Faidherbia* is included in the Ingeae.

Vassal's (1972) subgenus *Acacia* corresponds to Bentham's (1875) series *Gummiferae*, and is now treated as genus *Vachellia*. This group has a pantropical distribution and comprises about 200 species, with most occurring in Africa and South America, although 9 species occur naturally in Australia (Kodala & Wilson 2006). Vassal defined this subgenus on the presence of stipular spines and bipinnate leaves (characters also used by Bentham), as well as colporate-type pollen.

Vassal (1972) did not have enough data to include *Filicinae* in his study, but in Guinet and Vassal (1978), *Filicinae* was placed in subgenus *Aculeiferum* with Bentham's (1875) series *Vulgares*. Subgenus *Aculeiferum* has a pantropical distribution similar to subgenus *Acacia*. Only two species are indigenous to the Cape York Peninsula in Australia, and another two species have become naturalised in northern Australia (Ross 2001). Vassal (1972) defined subgenus *Aculeiferum* as having bipinnate leaves, simple porate pollen (although some species of *Vulgares* have extraporate pollen), prickles and an absence of stipular spines. He recognised three sections within subgenus *Aculeiferum*, but studied only 16 out of approximately 150 species (Conn *et al.* 1989).

Vassal's (1972) subgenus *Phyllodineae* comprised Bentham's (1875) series *Botrycephalae*, *Phyllodineae* and *Pulchellae*. These were described by Guinet (1969) as the "Australian group" and are largely confined to that continent (see Fig 1). Pollen in this subgenus is extraporate or sometimes simple porate, spinescent stipules are rare and prickles absent. The foliage may be bipinnate or phyllodinous. Vassal (1972) defined three sections in this subgenus, which combined subseries from Bentham's series *Phyllodineae* (members of which Vassal split into two sections) and *Botrycephalae*. Vassal's (1972) section *Pulchelloidea* included a heterogeneous arrangement of species from Bentham's (1875) series *Phyllodineae* and *Pulchellae* (excluding "plurinerved" species), based on seed and seedling characters. This reclassification included both bipinnate and phyllodinous species in *Pulchelloidea*.

2. *Acacia s.l.* studies prior to phylogenetic analyses

Pettigrew and Watson (1975) conducted a phenetic analysis of Australian *Acacia s.s.* (subgenus *Phyllodineae*) species and recommended disbanding Vassal's section *Pulchelloidea*. Their study showed that the phyllodinous species in this section were similar to species in Vassal's section *Phyllodineae*. However, in agreement with Vassal (1972), the bipinnate-leaved species in Bentham's series *Pulchellae* were found to be different from those in the *Botrycephalae*. Pettigrew and Watson (1975) suggested that Bentham's series *Pulchellae* is related to the phyllodinous subseries *Plurinerves*, and although they did not give an alternative to the placement of Bentham's series *Pulchellae*, they did recognise Vassal's sections *Phyllodineae* and *Uninerveae* as coherent groups.

Pedley (1978) supported Pettigrew and Watson's (1975) conclusions that the *Uninerveae* are a natural group, although he stated that their study was marred by some errors in identification. Guinet *et al.* (1980) addressed the problems Pettigrew and Watson (1975) identified regarding sect. *Pulchelloidea*. Guinet *et al.* provided evidence from adult morphology, pollen morphology, seed and seedling morphology and seed amino acids that supported Vassal's 1972 acceptance of Bentham's series *Pulchellae*. They disagreed with Pettigrew and Watson's (1975) assertion that the *Pulchellae* are closely related to subseries *Plurinerves*; instead they reaffirmed acceptance of Vassal's sect. *Pulchelloidea* containing phyllodinous and bipinnate species. Vassal and Rouane (1987) reanalysed the groupings within subgenus *Phyllodineae* on the basis of juvenile characters and found further evidence to support Vassal's 1972 groups. In a statistical analysis they found two clusters of species, one corresponding to Vassal's section *Heterophyllum* and the other to section *Pulchelloidea*.

A study of free amino acids in the seeds of 106 species of *Acacia s.l.* (Evans *et al.* 1977) also supported Vassal's 1972 division of *Acacia s.l.* into three subgenera. This study showed that species in subgenus *Acacia* contained the marker amino acid N-acetyldjenkolic acid, which was not found in subgenera *Aculeiferum* and *Phyllodineae*. The latter both contained the same combinations of marker amino acids: S-carboxyethylcystein, S-carboxyisopropylcystein, albizzine and α -amino- β -acetylamino propionic acid. Subgenus *Phyllodineae* was distinguished by the presence of an additional

amino acid, α -amino- β -oxalylaminopropionic acid. These data provided evidence that subg. *Phyllodineae* and subg. *Aculeiferum* are more closely related to each other than to subg. *Acacia*. Evans *et al.* (1977) disagreed with Vassal's (1972) transfer of *A. albida* into the genus *Faidherbia* and argued that amino acid data warranted its inclusion in *Acacia* subg. *Aculeiferum*.

Tindale and Roux (1969, 1974) conducted studies of the two main groups of flavonoids (the resorcinol type and the pyrogallol type) in the heartwood and bark of *Acacia s.s.* (subg. *Phyllodineae*). In subg. *Phyllodineae*, Tindale and Roux found pyrogallol flavonoids in Bentham's subseries *Plurinerves* and *Juliflorae* and resorcinol flavonoids in series *Botrycephalae*, *Phyllodineae* subser. *Brunioideae* and some ser. *Uninerves* (those with racemose inflorescences). A combination of both types of flavonoids were found in subg. *Phyllodineae* subseries *Continuae*, *Pungentes*, *Calamiformes* and the remaining *Uninerves*. Thus, Tindale and Roux's (1969, 1974) work supported Vassal's (1972) sect. *Uninerveae* (which contained Bentham's sections *Botrycephalae* and *Uninerves* with racemose inflorescences) due to the presence of resorcinol. Tindale and Roux considered pyrogallol flavonoids as originating from a resorcinol type precursor and therefore regarded resorcinol as being 'primitive'. Guinet and Vassal (1978) supported this interpretation and considered sect. *Uninerveae* as 'primitive' within subg. *Phyllodineae*. Pedley (1978), however, disagreed and proposed that it is equally likely that the 'primitive' group contained both flavonoid types. Tindale and Roux (1975) also hypothesised, based on a study of African species, that subg. *Acacia* was less "advanced" than subg. *Aculeiferum* because resorcinol flavonoids are most prevalent in subg. *Acacia* and less common in subg. *Aculeiferum*. In contrast, Ross (1973, 1981) found that a greater number of species in subg. *Acacia* displayed polyploidy, a character which he regarded as being more 'advanced'.

In an attempt to clarify the confusion surrounding 'primitive' and 'advanced' characters, Guinet and Vassal (1978) conducted an intuitive (non-cladistic) study of the "level of specialisation" within *Acacia s.l.* They examined pollen, chromosome number, the morphology of seeds, seedlings, pods, inflorescences and vegetative characters. Characters were divided into three states – unspecialised, specialised and highly specialised

– and applied to each of the subgenera recognised by Vassal (1972). From this information total levels of specialisation were estimated. Guinet and Vassal (1978) found that subg. *Acacia* was the most specialised and subg. *Aculeiferum* the least specialised. Ross (1981) and Pedley (1986) criticised the arbitrary size classes for the three states, and Pedley (1986) also disagreed with some of the evolutionary polarities to which the character states were assigned. For example, Pedley countered the interpretation that small seeds are unspecialised by giving evidence that seed predation may make smaller seeds an advanced state.

3. Pedley's splitting of *Acacia* s.l. and the ensuing controversy

Pedley (1978, 1979), in his first revision of *Acacia* s.l., assessed the data of Vassal (1972), chemical data from Tindale and Roux (1969, 1974, 1975) and Evans *et al.* (1977) and information on chromosome numbers, hairs, stipules, leaf, glands, inflorescences, flowers, pod and seed characters. Pedley (1978) recognised three subgenera that corresponded to those of Vassal (1972), but his scheme differed in the arrangement of sections within the three subgenera, ostensibly to make his classification more usable. Pedley (1978) advocated a more agglomerative approach than Vassal (1972) and reinstated some of Bentham's (1875) subseries within subgenus *Phyllodineae*. Pedley also named three sections in subg. *Acacia* instead of Vassal's two. The

main differences, however, between Pedley (1978) and Vassal (1972) reside in subg. *Phyllodineae*. Pedley created the new section *Lycopodiifoliae* to include species with phyllodes in whorls with interspersed stipules. These species were originally included in subser. *Brunioideae* Bentham, but were not studied by Vassal (1972). Pedley (1978) regarded uninerved and plurinerved phyllodes as the basis for a fundamental division in subg. *Phyllodineae*. Maslin (1988), disagreed, and gave examples of single species that may vary between uninerved and plurinerved states. However, Maslin (Maslin & Stirton 1997; Maslin 2001) later accepted there is a fundamental division between uninerved and plurinerved species. Pedley's (1978) infrageneric groups are those commonly used today (see Table 2 for a simplified key).

Pedley (1981), using data similar to those of his 1978 study but placing more emphasis on pollen, seedling and chemical characters, recommended splitting the genus into *Acacia*, (containing only subg. *Acacia*), and a genus "Z", which would include subg. *Phyllodineae* and subg. *Aculeiferum*. Later Pedley (1986), formally split *Acacia* s.l. into three genera, applying and resurrecting earlier generic names; subg. *Acacia* became genus *Acacia*, subg. *Phyllodineae* became *Racosperma* Martius and subg. *Aculeiferum* became genus *Senegalia* Rafinesque. The split was widely criticised at the time, despite Pedley's (1986, 1987b, 1987c) attempts to justify his scheme on the basis that many other large plant groups (such as Casuarinaceae) were in the process of similar changes.

Table 2. A simplified key to the classification of *Acacia* s.s. (formerly *Acacia* subgenus *Phyllodineae*, synonym *Racosperma*) by Pedley (1978) (adapted from Maslin 1995 and Arjati 2006).

1 Leaves (mature plants) reduced to phyllodes or scales, or absent	
2 Flowers arranged in cylindrical spikes	Section <i>Juliflorae</i>
2: Flowers arranged in globular or oblongoid heads	
3 Branchlets winged by decurrent phyllodes	Section <i>Alatae</i>
3: Branchlets not winged	
4 Phyllodes arranged in whorls	Section <i>Lycopodiifoliae</i>
4: Phyllodes not in whorls	
5 Phyllodes 1-nerved per face (4-7 nerved when terete or quadrangular)	Section <i>Phyllodineae</i>
5: Phyllodes more than 1-nerved per face (8 or more nerved when terete or quadrangular)	Section <i>Plurinerves</i>
1: Leaves of mature plants bipinnate	
6 Heads arranged in elongated racemes	Section <i>Botrycephalae</i>
6: Heads or axillary peduncles solitary	Section <i>Pulchellae</i>

Pedley (1986) stated that phylogeny and biogeography were being hampered by the acceptance of *Acacia s.l.* as a large, heterogeneous genus.

Maslin (1988), opposed Pedley's (1986) classification on the basis that the data Pedley used to change his interpretation in the years 1978 to 1986 were not significant enough to support such a substantial alteration. Maslin (1988) stated that Pedley (1986) incorrectly placed greater emphasis on certain characters to upgrade the infrageneric ranks in *Acacia s.l.* and was unduly influenced by trends in other plant groups. He maintained that Pedley's proposal was premature and more information was needed before any changes to the genus were made. Vassal (1988) supported Maslin's criticism of Pedley (1986), claiming that too many uncertainties remained in the recognition of coherent groups within *Acacia s.l.* Consequently, Pedley's (1986) concept and split of *Acacia s.l.* was not widely accepted until recent molecular results resolved many of the uncertainties (e.g. Miller *et al.* 2003b).

One aspect of Pedley's (1986) classification that was accepted was his suggestion that there had been an independent derivation (polyphyly) of at least two groups within *Acacia s.l.* Pedley (1986) thought subg. *Acacia* forms one group and subg. *Aculeiferum* plus subg. *Phyllodineae* (*Senegalia* plus *Racosperma*) the other. Only recently has it been possible to identify the closest relatives to these groups outside the tribe Acacieae. At the time, Guinet (1990) stated that pollen morphology clearly isolated subg. *Acacia* from the rest of the genus and placed it closer to the tribe Mimoseae. In contrast, Pedley (1986) regarded subg. *Aculeiferum* and subg. *Phyllodineae* as most closely related to the tribe Ingeae. This has been supported by recent results of Luckow *et al.* (2003). The relatively recent realisation that some taxa placed within *Acacia s.l.* were more closely related to other members of the Mimosoideae was a critical breakthrough (Chappill & Maslin 1995; Grimes 1995). Testing the monophyly of the three genera/subgenera of *Acacia s.l.*, and determining the sister relationships of these groups has become the goal of recent research.

Phylogenetic analyses of *Acacia s.l.*

The main reason why confusion previously surrounded the classification of *Acacia s.l.* was the lack of comprehensive cladistic analyses to investigate the

phylogenetic relationships both within the genus and at a higher level. As a first step, Playford *et al.* (1992) conducted a small comparative study of the 5S spacer ribosomal DNA in seven *Acacia s.l.* species and used cladistic methods to analyse their results. However, their study was deficient in sampling genera outside *Acacia s.l.* and therefore could not resolve any of the questions raised by Guinet (1990) and Pedley (1986). Playford *et al.*'s (1992) study found three paralogous copies of the 5S spacer rDNA units in the *Acacia s.l.* species they studied, making any analysis of the relationships between the three subgenera difficult. However, they did conclude that subg. *Phyllodineae* formed a cluster separate to subg. *Acacia* plus subg. *Aculeiferum*.

Chappill and Maslin (1995) used a morphological and chemical dataset to examine the tribal status of Acacieae in relation to other taxa in the Mimosoideae, as well as infrageneric relationships of *Acacia s.l.* Chappill and Maslin's (1995) generic analysis concluded that the tribe Acacieae was polyphyletic. *Faidherbia* and subg. *Acacia* nested within the Ingeae, whereas subg. *Aculeiferum* and subg. *Phyllodineae* were sister taxa and sister to the tribe Ingeae + *Faidherbia* and subg. *Acacia* clade. Thus, Chappill and Maslin (1995) proposed a unification of the tribes Acacieae and Ingeae, as suggested by Guinet (1969) on the basis of pollen morphology. However, Chappill and Maslin (1995) also conducted an 'infrageneric analysis', in which they found subg. *Aculeiferum* to be paraphyletic. A clade containing members of subgen. *Aculeiferum* section *Aculeiferum* and one exemplar of section *Monacanthae* was sister to a monophyletic subg. *Phyllodineae*. In this analysis *Faidherbia* was nested within subg. *Aculeiferum*, and subg. *Acacia* formed a clade. However at the basal node of the cladogram a clade of subgen. *Acacia* was unresolved with respect to a clade of tribe Ingeae taxa and another clade containing subgenera *Aculeiferum* and *Phyllodineae*. Robinson and Harris (2000) criticised the results of Chappill and Maslin (1995), remarking that their "generic" and "infrageneric" cladograms are contradictory in their placement of subg. *Acacia* and subg. *Aculeiferum*. The major limitation of Chappill and Maslin's (1995) dataset was the large proportion of missing data (approximately 28% in the infrageneric analysis), which can severely affect the number of equally parsimonious trees found in a cladistic analysis

(Kitching *et al.* 1998). In the only other substantial morphological cladistic analysis of the tribe Ingeae and tribe Acacieae, Grimes (1999) found that Acacieae was polyphyletic, with *Faidherbia* and subg. *Aculeiferum* and subg. *Acacia*, nested within tribe Ingeae. Subgenus *Phyllodineae* was sister to that (tribe Ingeae + subg. *Aculeiferum*/subg. *Acacia* + *Faidherbia*) clade.

Robinson and Harris (2000) used plastid DNA restriction fragment length polymorphisms (RFLPs) to examine the phylogeny of *Acacia s.l.* and the relationship of taxa of tribe Acacieae to taxa in tribe Ingeae. Robinson and Harris (2000) included 59 species of *Acacia s.l.*, seven species of tribe Ingeae, *Faidherbia* and one species of tribe Mimoseae in their study. The main sampling limitation was the number of taxa sampled from subg. *Phyllodineae* (*Acacia s.s.*): six species from only four of the seven sections were sampled. They found subg. *Phyllodineae* to be monophyletic and nested within a clade containing tribe Ingeae. *Faidherbia* was found to be sister to this clade. Robinson and Harris also found that both subg. *Acacia* and subg. *Aculeiferum* were monophyletic and sister groups.

Bukhari *et al.* (1999) obtained a different result from both Chappill and Maslin (1995) and Robinson and Harris (2000). They also used plastid RFLPs, but in contrast to Robinson and Harris (2000), they found subg. *Acacia* was sister to subg. *Phyllodineae*, and this clade was sister to another clade containing *Faidherbia* nested within subg. *Aculeiferum*. Bukhari *et al.* (1999) did not include any other members of the Mimosoideae in their analysis, precluding the possibility of finding sister group relationships of *Acacia s.l.* to taxa outside the tribe Acacieae.

Miller and Bayer (2000, 2001) conducted molecular phylogenetic analyses using chloroplast (*trnK/matK*) and nuclear (histone H3-D) DNA sequences. Their studies included taxa from tribes Acacieae and Ingeae, and a few tribe Mimoseae taxa. Miller and Bayer found that the Ingeae were paraphyletic by inclusion of a monophyletic *Acacia s.s.* They also found that *Faidherbia* was sister to the *Acacia s.s.* + Ingeae clade and subg. *Acacia* (*Vachellia*) was monophyletic and sister to *Neptunia*, to a member of the Mimoseae. Subgenus *Aculeiferum* was paraphyletic, with *A. boliviana* (section *Filicinae*) resolved at the basal node, sister to the ingroup.

More recently, with greater sampling of diversity

in the tribes Ingeae, Acacieae and Mimoseae and the use of multiple chloroplast DNA regions, greater congruence has been found between the studies by Luckow *et al.* (2003) and Miller *et al.* (2003b). These studies have shown that subg. *Acacia* (*Vachellia*) is well supported as monophyletic and related to members of tribe Mimoseae, well removed from other members of *Acacia s.l.* or tribe Ingeae. The tribe Ingeae and members of subg. *Aculeiferum s.l.* were paraphyletic. *Acacia s.s.* was strongly supported as monophyletic and nested amongst tribe Ingeae, although its relationship to members of tribe Ingeae was unresolved.

Phylogenetic relationships within *Acacia s.s.* and comparison with earlier classifications

In recent years and in multiple analyses (Chappill & Maslin 1995; Grimes 1999; Bukhari *et al.* 1999; Robinson & Harris 2000; Miller & Bayer 2000, 2001; Luckow *et al.* 2003; Miller *et al.* 2003b) most of the possible combinations of relationships between the three subgenera in *Acacia s.l.* and the tribe Ingeae have been hypothesised. The recent use of DNA sequence data has provided more congruent results and the clear realisation that *Acacia s.s.* is monophyletic. There have now been a number of recent phylogenetic studies that have focussed on this, mostly Australian, clade, however, little was known about the relationships of taxa within this large heterogeneous arrangement of species (Chappill & Maslin 1995; Bukhari *et al.* 1999; Robinson & Harris 2000; Miller & Bayer 2000, 2001). *Acacia s.s.* is generally divided into seven sections (Pedley 1978; see Table 2). However, uncertainty has surrounded infrageneric groups (Bentham 1875; Vassal 1972; Pedley 1978, 1986), and at least one section, *Alatae*, was thought not to be monophyletic by Maslin and Stirton (1997). Chappill and Maslin (1995) found that the classification within subg. *Phyllodineae* needed to be re-assessed. Vassal's (1972) sect. *Pulchelloidea* was not supported in their analysis, and none of Pedley's (1978) sections within subgenus *Phyllodineae* were resolved as monophyletic.

There is currently no phylogenetically based classification of *Acacia s.s.* despite the size, conspicuousness and importance of the group within Australian ecosystems (Hnatiuk & Maslin 1988, Maslin 2001). The sheer size of *Acacia s.s.*, with over 975 species, makes a comprehensive analysis of the whole genus

difficult. It is likely that the approach of examining the phylogeny of smaller groups of taxa will incrementally improve knowledge, and by using DNA datasets, such as chloroplast and nuclear ribosomal (ITS and ETS) DNA sequences (e.g. Murphy *et al.* 2000, 2003; Ariati *et al.* 2006; Brown *et al.* 2006) it has been possible to build on previous studies. This approach is only limited by the relative informativeness of molecular markers at different taxonomic levels. Some conclusions on relationships within *Acacia s.s.* can now be made, although it is currently premature to undertake formal taxonomic changes.

For comparative purposes the studies of *Acacia s.s.* below will be discussed in light of the sections of Pedley (1978). Although it is difficult to compare the various phenetic and cladistic analyses that have been conducted over the last 40 years with more recent DNA based phylogenies – due to limited overlap of sampling and differing methods – some congruence of results is now apparent. The sections in *Acacia s.s.*, which were defined by Bentham (1875) and later re-aligned by Pedley (1978) and subsequent workers (see Table 1), are now known to be largely unnatural but form a pragmatic and easily used system (Maslin 2001). The groups defined by Vassal (1972) (not including sect. *Lycopodiifoliae* which were not considered in that study), are similar to the groups defined by Pedley (1986). Both Vassal (1972) and Pedley (1986) amalgamated the *Botrycephalae* with section *Phyllodineae* into one section, and the *Plurinerves* and *Juliflorae* into another section, to form two very large sections (Table 1). However, their treatments differed in the classification of the remaining taxa in *Acacia s.s.*, especially sections *Alatae* and *Pulchellae*.

Overall, four main groups of taxa have been resolved in recent molecular phylogenies using DNA sequences (e.g. Murphy *et al.* 2000, 2003, 2005; Miller *et al.* 2003a). These groups are briefly outlined below and followed by more detailed comparisons to the results of previous studies:

- A clade comprising sections *Lycopodiifoliae*, *Alatae*, *Pulchellae* and some *Phyllodineae*. This group is probably one of the most significant findings of recent years because it provides support for a similar group to Vassal's (1972) sect. *Pulchelloidea*.
- A large clade containing species with plurinerved

phyllodes, in sections *Juliflorae* and *Plurinerves*, and many uninerved taxa (sect. *Phyllodineae*), more typically the non-racemose species.

- Nested within the above plurinerved clade is a smaller clade containing all members of sect. *Botrycephalae* and some members of sect. *Phyllodineae*, typically those with racemose inflorescences (Brown *et al.* 2006).
- Recently two clades of mostly arid zone taxa have been resolved. These groups contain species related to *Acacia victoriae*, *Acacia pyrifolia* (the "Acacia victoriae clade") and *Acacia murrayana* (the "A. murrayana clade"). While these taxa form two well supported clades, their placement in relation to other taxa in *Acacia s.s.* remains equivocal (Ariati *et al.* 2006).

Pulchelloidea clade

Within *Acacia s.s.* only one section, sect. *Lycopodiifoliae*, has been supported as monophyletic. The other sections were found to be non-monophyletic or there was not enough information to confirm or refute a hypothesis of monophyly. Section *Lycopodiifoliae* (Bentham's subseries *Bruniodeae*), which have phyllodes in whorls, are morphologically distinct from other taxa in *Acacia s.s.* Rutishauser (1999) demonstrated that the phyllode and stipule whorls in sect. *Lycopodiifoliae* are developmentally unique and Pedley (1987a) suggested that it was likely that sect. *Lycopodiifoliae* would be segregated from subg. *Phyllodineae*, although it is now apparent that the segregation of sect. *Lycopodiifoliae* would leave *Acacia s.s.* paraphyletic (Murphy *et al.* 2003). However, so far the monophyly of sect. *Lycopodiifoliae* has not been thoroughly explored. Chappill and Maslin (1995), in their morphological analysis, used a single representative from this section, and found that it grouped with taxa in sect. *Plurinerves*. In contrast, Brain and Maslin (1996), using serological data, concluded that sect. *Lycopodiifoliae* may be closely related to sect. *Juliflorae*. The study by Brain and Maslin (1996) was the most comprehensive molecular study of *Acacia s.s.* prior to recent DNA sequence analysis, although the serological method was limited by the requirement for simultaneous analysis of samples. Vassal (1972) did not include any representatives of sect. *Lycopodiifoliae* in his study. Pettigrew and Watson (1975) conducted

a phenetic analysis, using the classification of Vassal (1972), and found that members of sect. *Lycopodiifoliae* grouped together. It was unclear, however, in Pettigrew and Watson's (1975) analysis whether sect. *Lycopodiifoliae* grouped with Vassal's (1972) sect. *Uninervea* (containing sections *Phyllodineae* and *Batrycephalae*) or sect. *Heterophyllum* (containing sections *Juliflorae* and *Plurinerves*).

Section *Pulchellae* are also morphologically distinct, with bipinnate foliage and often with stipular spines (Guinet *et al.* 1980). Somewhat surprisingly sect. *Pulchellae* have not been confirmed as monophyletic (e.g. Murphy *et al.* 2003; Miller *et al.* 2003a). However, like sect. *Lycopodiifoliae* the sampling of sect. *Pulchellae* has been limited in molecular analyses. Vassal's (1972) sect. *Pulchellaidea* was based on seedling, pollen and other morphological characters (including spinescent stipules), and included members of sections *Pulchellae*, *Alatae* and other taxa from sect. *Phyllodineae*. Chappill and Maslin (1995) thought it likely that the only groups to be monophyletic were the two sections with bipinnate foliage, sect. *Batrycephalae* and sect. *Pulchellae*, although both these sections were unresolved in their morphological analysis. Chappill and Maslin (1995) found that sect. *Pulchellae* grouped in a clade with some members of sections *Alatae* and *Phylladineae* with non-racemose inflorescences. Brain and Maslin (1996) found "no strong relationship" of sect. *Pulchellae* with any other group in subg. *Phyllodineae* but a weak association between sect. *Alatae* and taxa in sections *Plurinerves*, *Juliflorae* and *Phyllodineae*. Maslin and Stirton (1997) concluded that sect. *Alatae* is an unnatural group.

Plurinerved taxa

Most members of *Acacia* s.s. have plurinerved phyllodes (sect. *Juliflorae* and sect. *Plurinerves*) but unfortunately there has been very little resolution of relationships of these taxa in phylogenetic studies. Although most plurinerved taxa are found in a single clade, their monophyly has not been supported by sequence data. DNA sequence studies have found a large clade, containing most members of sections *Juliflorae* and *Plurinerves* and members of sect. *Phyllodineae* and *Batrycephalae* (Murphy *et al.* 2003; Miller *et al.* 2003a). However, there is little resolution within this large clade,

apart from the relationship of sections *Batrycephalae* and *Phyllodineae* with racemose inflorescences (described below). While many studies have found a natural division between taxa with single-nerved phyllodes (sect. *Phyllodineae*) and those with plurinerved phyllodes (Vassal 1972; Pettigrew & Watson 1975; Pedley 1986; Chappill & Maslin 1995; Maslin & Stirton 1997; Miller & Bayer 2000), Brain and Maslin (1996) did not find a clear distinction between the uninerved and plurinerved taxa using serological data. Additionally, there has not yet been any phylogenetic study that supports the informal groupings of oligoneurous and microneurous taxa. These are taxa with differing arrangements of minor secondary nerves in their phyllodes, in sections *Juliflorae* and *Plurinerves* (Maslin & Stirton 1997, see Table 1).

Batrycephalae

A close relationship of taxa from sect. *Batrycephalae* to taxa in sect. *Phylladineae* with racemose inflorescences was hypothesised in a number of earlier studies, such as those using: flavonoid chemistry (Tindale & Raux 1969, 1974), morphology (Vassal 1972; Chappill & Maslin 1995) and more recently DNA sequence data (e.g. Murphy *et al.* 2000). The large-scale phylogenies of *Acacia* s.s. by Murphy *et al.* (2003) and Miller *et al.* (2003a) provided increased evidence for the relationship of sect. *Batrycephalae* to some taxa in sect. *Phylladineae*, and it was confirmed by Brown *et al.* (2006), whose comprehensive analysis showed that sect. *Batrycephalae* is polyphyletic, and nested within sect. *Batrycephalae* are taxa of sect. *Phyllodineae* with racemose inflorescences.

Much speculation has focussed on whether bipinnate leaves in mature plants are plesiomorphic in *Acacia* s.s. because adult bipinnate foliage is a widespread character in subfamily Mimosoideae (Guinet and Vassal 1978; Mound and Crespi 1999). Mapping of morphological characters onto molecular phylogenies does not support the conclusion that adult bipinnate foliage is plesiomorphic (Murphy *et al.* 2000, 2003, Miller *et al.* 2003a). The only bipinnate sections, *Batrycephalae* and *Pulchellae*, are not sister groups and are both nested within clades of phyllodinaus taxa, which indicates that two separate reversals to bipinnate leaves have occurred (Murphy *et al.* 2003). The reversal to bipinnate foliage (compound leaves) may be interpreted as neatenous, since the antogeny of phylladinaus taxa includes a

pinnate phase (Pedley 1986). Pedley (1986) recognised that sect. *Botrycephalae* may be neotenic because of the occurrence of transitional taxa, such as *A. latisejala* Pedley, which only sometimes produce phyllodes.

Conclusion

Problems have been apparent in the systematics and classification of *Acacia s.l.* for many years (Maslin & Stirton 1997). Early literature was centred on taxonomic lists of *Acacia s.l.* species without consideration of relationships between the taxa. However, Bentham (1875) created a classification of *Acacia s.l.* that was robust enough to last almost a century, although concerns over the last thirty years have necessitated revision of this classification. Vassal (1972) recognised three subgenera within *Acacia s.l.* Pedley (1986) revised the genus and formalised three genera corresponding to Vassal's subgenera, but this reclassification was regarded as premature at the time of its publication, and other workers advised caution before such an important nomenclatural decision was made (Maslin 1988; Vassal 1988; Chappill & Maslin 1995). Chappill and Maslin (1995) published the first cladistic analysis of the genus, in which they recognised *Acacia s.l.* as paraphyletic and stated that their findings lent support to previous authors' suggestions (such as those of Guinet 1969 and Pedley 1981) and proposals (Pedley 1986) to divide *Acacia s.l.* into more than one genus. In recent years the polyphyly of *Acacia s.l.* has been well demonstrated and the monophyly of *Acacia s.s.* supported (Luckow *et al.* 2003; Miller *et al.* 2003b; Murphy *et al.* 2003). It has been recognised that a phylogenetic classification of *Acacia s.s.* is required (e.g. Maslin & Stirton 1997, Maslin 2001), and molecular phylogenetic studies of recent years have clarified the relationships of groups within *Acacia s.s.* (Miller *et al.* 2003a, Murphy *et al.* 2003). However, further studies with increased sampling across the diversity of *Acacia s.s.*, and additional molecular markers are required to provide a comprehensive understanding of the phylogeny of *Acacia s.s.* and to resolve clades for a revised classification. In the past, single morphological characters or combinations of characters, such as the number of phyllode nerves and inflorescence characters, have been used to define groups in *Acacia s.s.* (Bentham 1875; Vassal 1972; Pedley 1978; Maslin & Stirton 1997). It has now been found that taxonomic groups in *Acacia*

s.s. based upon one or two "key" characters are not monophyletic and the characters used to define them are homoplasious.

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